

## Comparative Locomotion and Habitat Use of Six Monkeys in the Tai Forest, Ivory Coast

W. SCOTT MCGRAW\*

Department of Anatomy, New York College of Osteopathic Medicine,  
Old Westbury, New York 11568

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**ABSTRACT** The relationships between locomotion, body size, and habitat use in six sympatric Old World monkeys are examined to test whether the associations found are consistent with those demonstrated in previous studies (Fleagle and Mittermeier [1980] *Am. J. Phys. Anthropol.* 52:301–314; Gebo and Chapman [1995] *Am. J. Phys. Anthropol.* 97:49–76). *Colobus polykomos*, *C. badius*, *C. verus*, *Cercopithecus diana*, *C. campbelli*, and *Cercocebus atys* were studied for 14 months in the Ivory Coast's Tai Forest. Analyses reveal that (1) larger monkeys tend to frequent those strata containing the greatest densities of large supports while smaller monkeys are more diverse in their canopy use; (2) high frequencies of leaping are not necessarily confined to the understory, and understory specialists are not necessarily frequent leapers; (3) body size does not consistently predict leaping or climbing frequencies; (4) in general, climbing is more frequent during foraging and leaping is more common during travel; (5) larger supports are used during travel while smaller supports are used during foraging; and (6) larger monkeys do not always use larger supports than do smaller monkeys. Some of the factors contributing to the manner that locomotion, body size, and habitat use are related in cercopithecoid monkeys are discussed. *Am J Phys Anthropol* 105:493–510, 1998. © 1998 Wiley-Liss, Inc.

In their influential work on Surinam monkeys, Fleagle and Mittermeier (1980) examined the relationships between a suite of locomotor and habitat variables, "in hopes that [their] natural experiment [would] yield results that are representative for understanding locomotor evolution throughout the order (1980:301)." These authors sought answers to fundamental questions such as the following: (1) Is there a general relationship between body size and locomotion? (2) Do locomotor patterns vary predictably with habitat? (3) Is there a functional relationship between body size and support size? Their conclusions (discussed below) served as working hypotheses that could be tested across all primate groups, and many researchers have subsequently investigated at

least some of the relationships between locomotion and/or body size, morphology, and ecology within prosimians (e.g., Gebo, 1987; Dagosto, 1989, 1992; Warren, 1997), platyrrhines (e.g., Garber, 1980, 1991; Fleagle et al., 1981; Cant, 1986; Gebo, 1992), apes (e.g., Cant, 1987; Doran, 1993; Hunt, 1992a,b), and catarrhine monkeys (e.g., Rose, 1979; Cant, 1988; Cannon and Leighton, 1994).

Despite this accumulation of evidence, there have been relatively few attempts to evaluate Fleagle and Mittermeier's original

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\*Correspondence to: W. Scott McGraw, Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, NY 11568. E-mail: smcgraw@iris.nyit.edu

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conclusions as they pertain to groups of sympatric primates. One exception is the recent study by Gebo and Chapman (1995). These authors studied five cercopithecids in Uganda's Kibale Forest and found that a number of the relationships demonstrated by Feagle and Mittermeier did not hold up. For example, it was demonstrated that (1) smaller species leaped less and climbed more than did larger species, (2) most leaping was observed in the mid- to upper canopy rather than in the understory, and (3) there was not a consistent relationship between body size and support use. In surveying available data on platyrrhines (Feagle and Mittermeier, 1980) and Asian cercopithecids (Rodman, 1979; Feagle, 1980; Cant, 1988), Gebo and Chapman concluded that there are "few consistent trends with respect to body size or habitat use across primates (1995:49)."

This study constitutes an additional test of the relationships between locomotion, body size, and habitat in a group of West African cercopithecoid monkeys. Specifically, I address the relationship between (1) body size and locomotion, (2) locomotion and maintenance activities, (3) body size and strata use, (4) locomotor behaviors within specific forest strata, (5) body size and support use, and (6) support use and maintenance activities.

## METHODS

Data were collected in the Tai National Park, Ivory Coast from June 1993 to August 1994. The park, located between 6° 20' N to 5° 10' N and 4° 20' W to 6° 50' W is the last remaining major block of rain forest in West Africa and consists of approximately 330,000 hectares of forest. Average rainfall is 1,830 mm, and the year is characterized by two dry seasons (July to August and November to February). Mean annual temperature is 24°C. The study site is located near the field station of the Institut de la Ecologie Tropicale (IET) of the Ministère d'Enseignement Supérieur et Recherche Scientifique of Ivory Coast. This research station, near the western boundary of the park, is approximately 25 km from the Liberian border. The core study area covers approximately 1 km<sup>2</sup> of moist, evergreen rain forest and has been described elsewhere (McGraw, 1996).

Six monkey species were studied<sup>1</sup>: *Colobus polykomos*, western black and white colobus (8.3 kg), *Colobus badius*, red colobus (8.2 kg), *Colobus verus*, olive colobus (4.2 kg), *Cercopithecus diana*, diana monkey (3.9 kg), *Cercopithecus campbelli*, Campbell's guenon (2.7 kg), and *Cercocebus atys*, sooty mangabey (6.2 kg). All species except for *Cercocebus atys* were fully habituated. The mangabey group was nearly fully habituated: i.e., all individuals except for a few subadults could be approached to within 5 and 10 m. Because all of these monkey groups contained more adult females than males, the former were chosen as focal animals to increase the sampling pool and to decrease the amount of time between time points required to sample another independent individual. Positional behavior of females was sampled at every 3-minute time point, and the same individual was not sampled within 15 minutes of itself to assure independence of data points.

Species were sampled on a rotating, weekly basis. When possible, a species was sampled continuously for 5 consecutive days before switching to the next species. Every attempt was made to sample species evenly throughout the length of the study in order to minimize any possible seasonal effect. Each morning, the focal species was located in its sleeping tree and followed all day until a sleeping tree (or location) for that night had been selected. The next morning, I returned to where I had left the focal species, and resumed sampling. On those occasions when the previous day's focal species could not be located, I attempted to locate and sample the next week's species. If the previous day's focal species was subsequently found, I resumed sampling it until that species' week of sampling was completed. At every 3-minute time point, I recorded the following:

1. Maintenance activity (i.e., feeding, resting, traveling, foraging),
2. Locomotor behavior (after Feagle, 1977): [*quadrupedal walking* (slow, quadrupedal, pronograde locomotion), *quadrupedal running* (fast gaits including bounding and

<sup>1</sup>Data on body weights (adult females) are from Oates et al. (1990).

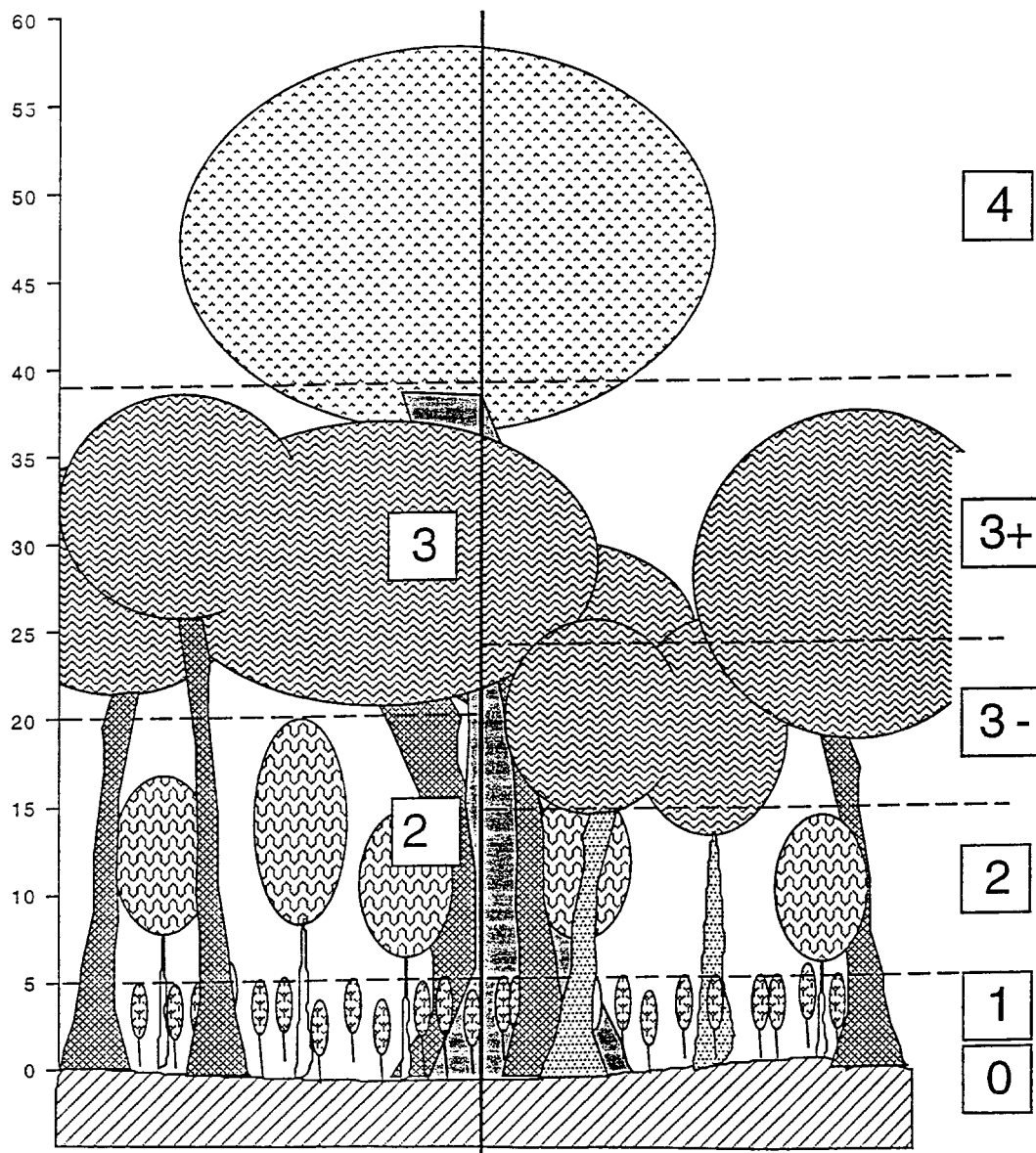


Fig. 1. Strata in the Tai Forest. Numbers at left are height in meters; numbers at right are corresponding strata categories.

galloping), *leaping* (progression between discontinuous supports using primarily rapid extension of the hindlimbs for propulsion . . . landing involves use of both hindlimbs and forelimbs), *climbing* (vertical ascent in which the arms reach above the head and pull the animal up while the hindlimbs alternatively push the body up), and *arm swinging* (loco-

motion involving forelimb suspension: bi-manualism)],

3. Forest strata (Fig. 1): broken into (a) *ground*, (b) *shrub and sapling layer* up to 5 m in height, (c) *understory* (small trees and half grown canopy trees usually between 5 and 15/20 m), (d) *main canopy* (closed canopy dominated by larger, more horizontal sup-

ports; divided further into lower main canopy usually between 15 and 23 m, and upper main canopy usually between 24 and 40 meters), and (e) *emergent layer* (largest trees that punctuate the main, continuous canopy; usually greater than 40 m),

4. Support type (after Fleagle, 1976): *boughs* (large supports usually greater than 10 cm in diameter in which grasping with hands or feet is not possible), *branches* (medium-sized supports between 2 and 10 cm in diameter permitting grasping of hands or feet), and *twigs* (small, flexible terminal branches usually less than 2 cm in diameter) and,

5. Location (i.e., grid cell).

The methods used to obtain data on the availability of different-sized supports at different forest levels are discussed in detail in McGraw (1996). Data were analyzed using SAS (SAS Institute Inc., 1985) and BIOM (Rohlf, 1982–1987). Significance tests ( $P = .01$ ) were performed on raw data using G tests with Williams correction (Sokal and Rohlf, 1981). The G statistic tests the goodness of fit of frequency rather than continuous data (see Sokal and Rohlf, 1981) and has been used in the analysis of locomotor data previously (Doran, 1992a,b, 1993). It is noted that sample sizes for certain activities and species are substantially lower than for others (e.g., leaping in *Cercocebus atys*). Interspecific comparisons were, therefore, not performed in those cases in which  $N < 10$ .

A number of factors account for the disparity in sample size between species. Differences in the number of adult females combined with the restriction that no female be sampled within 15 minutes of herself limited, in many instances, the number of data points that could be taken on a given day and, consequently, throughout the course of the study. Particular care was taken to avoid sampling females within 15 minutes of themselves, a restriction requiring the ability to recognize individuals. In addition, even for those species with a large number of adult females, it was not always possible to locate and positively identify a female that had not been sampled within the previous 15 minutes. On these occasions, no data were taken and sampling resumed only when a female meeting the above criteria was found.

An additional factor contributed to the comparatively small sample size in *Cercocebus atys*. The home ranges of the arboreal species are completely contained within the 1-km<sup>2</sup> study grid (McGraw, 1996). In contrast, the mangabey home range is estimated at approximately 6–7 km<sup>2</sup> (McGraw, unpublished data) and thus extends far beyond the grid in which sampling of the other taxa took place. I chose to sample mangabeys only when they ranged within the grid; however this restriction should have little, if any, effect on the locomotor profiles of *Cercocebus atys* since it has been shown that (1) the locomotion of the Tai monkeys is conservative with respect to habitat (McGraw, 1996), (2) seasonal differences in feeding do not significantly alter the strata use of mangabeys to the extent that they might influence frequencies of climbing, leaping, etc. (Bergmueller, personal communication), and (3) Tai monkeys are predominantly terrestrial year round, both within and outside the grid (Bergmueller, personal communication).

The sampling regime employed in this study was designed specifically to avoid the problems of data dependency common in field studies of positional behavior as outlined by Dagosto (1994). Specifically, (1) time-point data were collected on individuals that were rotated (and not sampled sequentially), (2) time-point data were taken at 3-minute intervals (not at intervals between 5 seconds and 2 minutes) and, (3) the same individual was not sampled within 15 minutes of itself. As discussed further by Dagosto (1994), a sampling pool consisting of a limited number of individuals is potentially an additional source of non-independence. For this reason, a reduced  $P$  value of .01 was employed to account for the comparatively small number of adult females in some species (e.g., *Cercopithecus campbelli*, *Colobus verus*). Further, to ensure that the Tai positional data were not temporally autocorrelated, a test for independence on all species was performed on postural frequency data. This test is designed to determine whether an observation at time  $X + 1$  is associated with the preceding observation at time  $X$ . As detailed in McGraw (1996), the 3-minute time-point postural data were shown to be independent, and it is therefore



highly unlikely that the locomotor data exhibit dependency. The whole data set could therefore be used.

## PREDICTIONS

### Body size and locomotion

Size is unquestionably a major influence on locomotion. One of Fleagle and Mittermeier's (1980) most important conclusions was that there are strong correlations between body size and locomotion, and they discussed the theoretical reasons why different-sized primates move in different ways through the same habitat (Napier, 1967; Cartmill, 1974; Crompton, 1984). Cant (1992) hypothesizes that primates seek to straighten the path of movement within trees while increasing the speed along the path of movement. If true, then different-sized primates confronted by the same arboreal architecture will move in different, though predictable, ways within the same habitat. In the case of the Tai monkeys, as body size increases, the amount of leaping should decrease while the amount of climbing should increase.

### Locomotion and maintenance activities

The locomotor behaviors used during travel differ from those used during foraging (e.g., Rose, 1977; Susman 1984; Hunt, 1992a). This is because during travel, "the endpoints are more general . . . the animals appear to choose regular pathways . . . that permit long uninterrupted bouts of locomotion on relatively stable supports. By contrast, the endpoints of locomotor bouts during feeding are more precise and to a large degree predetermined by the location of the food sources on the relatively small terminal branches (Fleagle and Mittermeier, 1980: 307)." Because food is often distributed on thin, unstable supports, reaching it requires a versatile behavioral repertoire. Climbing, therefore, assumes a more important role in foraging than during travel. If monkeys choose to minimize the distance traveled by straightening pathways (Cant, 1992), they may more regularly encounter discontinuities in the canopy which can only be crossed by bridging or leaping. We would therefore expect more leaping and less climbing behav-

ior during travel and a preponderance of quadrupedalism.

### Body size and forest strata

Napier (1962) argued that the varying abundance of different-sized supports in different strata facilitates certain kinds of movement while limiting others. While it may be possible to predict where specific locomotor *behaviors* are most likely to take place within the forest strata (e.g., Cannon and Leighton, 1994) (see below), predicting where different-sized monkeys are most likely to be found is more complex. For example, there is little doubt that different primates prefer different forest levels (e.g., Terborgh, 1983; McGraw, 1994; Ungar, 1996). Among sympatric monkeys, foraging constraints (Cords, 1987), predation (Gautier-Hion et al., 1981, 1983), and interspecific competition (Janson and Boinski, 1992; Quiris, 1976; Gautier-Hion, 1988a,b) have all been used to explain why different species are found at different forest levels. However, a *general* rule has yet to be demonstrated that predicts where different-sized arboreal quadrupeds are most likely to locomote, independent of one or more ecological factors. Therefore, I will draw upon results from a canopy survey (McGraw, 1996) to predict strata use on the basis of the proposed relationship between body size and support size (see below). In doing so, I fully acknowledge that support size is unlikely to be the sole determinant of canopy use. Nevertheless, by relating general strata use to the relative abundance of different-sized supports at different heights, it should be possible to begin understanding the extent that a monkey's position in the forest is influenced by differences in support abundance. If substrate size limits quadrupedal locomotion, then large-bodied quadrupeds are more likely to be found in the main canopy where large supports are generally more abundant (Richards, 1952). Smaller monkeys, because of the ratio of support to body size, are able to utilize a greater number of support types and can, consequently, more easily exploit more forest layers and will thus tend to be more widely distributed throughout all forest strata.

### Locomotion and forest strata

The forest understory is dominated by discontinuous, vertical supports which generally preclude high frequencies of quadrupedalism. In theory, primates moving through this forest layer are most often required either to leap from one vertical support to another or to climb between supports. In contrast, the main canopy is characterized by an interlocking network of more continuous supports which would seem to promote quadrupedalism across more horizontally oriented arboreal pathways. The top of the main canopy and the emergent layers are characterized by thinner, less stable, discontinuous supports. Movement through this highest forest level more likely requires leaping and/or climbing. Thus, climbing and leaping should occur at those forest levels (e.g., understory and emergent levels) where quadrupedalism is not possible (i.e., where the abundance, distribution, and size of supports precludes horizontal travel across stable, continuous supports).

### Body size and support use

For a series of different-sized arboreal, quadrupedal primates (lacking specializations such as prehensile tails or claws) there should be a clear association with the size of supports used: Large-bodied monkeys should demonstrate a preference for large substrates to better support their weight and maintain their center of gravity above the support. Smaller-bodied primates, because of the ratio between their size and the number of available supports, should have a greater number of substrates to chose from. For this reason, small-bodied quadrupeds should be less restricted in their support choice and will therefore use a greater variety of different-sized supports.

### Support size and maintenance activities

Maintenance activities should also bear upon the size of supports used. If preferred food items tend to be distributed among the slender, flexible supports found in the periphery of tree crowns, then supports used during foraging (locomotion while feeding) should generally be smaller than those used during traveling. Thus, during travel, mon-

TABLE 1. Locomotor profiles during overall locomotion, travel, and foraging<sup>1</sup>

Species	AS	CL	L	QR	QW	N
<i>Colobus badius</i>						
Overall	3.9	17	17.8	8.2	53.1	1,466
Travel	2.9	12.2	20.8	9.3	54.8	797
Forage	5	21.6	15	5	53.4	669
<i>Colobus polykomos</i>						
Overall	—	14.3	14.5	29.4	41.8	918
Travel	—	8	17.6	31.8	42.6	538
Forage	—	24.2	13.3	12	50.5	380
<i>Colobus verus</i>						
Overall	—	12	20.4	22.4	45.2	508
Travel	—	6.3	25	29.6	39.1	306
Forage	—	20.8	13.5	10.5	54.5	202
<i>Cercopithecus diana</i>						
Overall	.1	19.4	10.4	10.8	59.3	1,553
Travel	—	6.2	16.7	23.8	53.3	242
Forage	.1	21	9.4	7.9	61.6	1,311
<i>Cercopithecus campbelli</i>						
Overall	—	14.5	5.2	7.7	72.6	596
Travel	—	3.1	5.2	23	68.8	96
Forage	—	16.4	5.2	4.8	73.5	500
<i>Cercocebus atys</i>						
Overall	—	12.5	1.02	5.7	80.7	466
Travel	—	2.9	.72	5.1	91.3	137
Forage	—	16.5	1.2	.9	81.4	329

<sup>1</sup> Data under each column are the percentages of locomotor time overall, during travel, and during foraging that each behavior was observed. AS, Arm Swing; CL, climb; L, leap; QR, quadrupedal run (including Bound); QW, quadrupedal walk. All interspecific comparisons of overall locomotion are significant except *Colobus polykomos* × *C. verus* [ $G = 7.5$ ]. All interspecific comparisons of locomotion during travel are significant except *C. polykomos* × *C. verus* [ $G = 6.3$ ], *C. polykomos* × *Cercopithecus diana* [ $G = 8.2$ ], *C. diana* × *Colobus verus* [ $G = 11.9$ ], and *Cercopithecus diana* × *C. campbelli* [ $G = 11.9$ ]. All interspecific comparisons of locomotion during foraging are significant except *C. polykomos* × *C. verus* [ $G = 1.2$ ] and *C. verus* × *Cercopithecus diana* [ $G = 6.5$ ].

keys will tend to seek out larger (though not necessarily more abundant) supports on which to move longer distances. This prediction should apply to all monkeys independent of body size and/or diet.

## RESULTS

### Body size and locomotion

The amount of time each species engaged in each locomotor activity is reported in Table 1. Regardless of whether overall locomotion (combined travel and foraging), locomotion during travel or locomotion during foraging is considered, colobines leap more than cercopithecines. All three colobus monkeys have greater body masses than two of the three cercopithecines, and two colobines have greater body masses than all three cercopithecines. Thus, when the six cercopithecids are considered together, body size

does not predict leaping frequencies the way it does among Fleagle and Mittermeier's platyrrhines (1980). Rather, among the arboreal Tai cercopithecids (*Cercocebus atys* is a predominantly terrestrial monkey), as body mass increases, so too do frequencies of leaping.

Examining trends within groups further complicates matters. Among colobines, the smallest (*Colobus verus*) is a more active leaper during overall locomotion and during travel. During foraging, on the other hand, the red colobus (*C. badius*) leaped more than the similarly sized black and white colobus (*C. polykomos*) as well as the considerably smaller olive colobus. Among cercopithecines, the largest (*Cercocebus atys*) was the least frequent leaper regardless of the maintenance activity. Even among arboreal cercopithecines, the larger *Cercopithecus diana* always leaped more often than the smaller *Cercopithecus campbelli*. Thus, although the largest cercopithecine leaped the least, the smallest (Campbell's monkey) never leaped the most.

The relationship between body size and climbing frequencies is also equivocal. Examining overall locomotor frequencies reveals that the most frequent climber was not the largest monkey (*Colobus polykomos*), but one of the smallest (*Cercopithecus diana*). Further, the smallest monkey (*Cercopithecus campbelli*) climbed slightly more than the largest (*Colobus polykomos*). During travel, the arboreal monkeys fit the predicted pattern: Climbing frequencies increase with body size. This pattern is less straightforward when foraging is considered: The smaller *Colobus verus* and *Cercopithecus diana* climbed in amounts similar to those of the larger red colobus. Climbing frequencies were similar in *Cercopithecus campbelli* and *Cercocebus atys* despite vastly different body sizes.

The prediction that larger monkeys will climb more than smaller ones is borne out when only colobines are examined: *Colobus badius* and *C. polykomos* climbed more than *C. verus* overall, as well as during travel and foraging. Among cercopithecines, however, the fit is less good: Despite being intermediate in size to *Cercopithecus campbelli* and *Cercocebus atys*, *Cercopithecus diana* was

the most frequent climber overall as well as during travel and foraging. Furthermore, *Cercocebus atys*, the largest monkey, climbed the least overall as well as during travel.

### Locomotion and maintenance activities

As predicted, climbing is used more frequently by all species during foraging than during travel (Table 1). In five of six species, leaping was used either the same amount (*Cercopithecus campbelli*) or more frequently (*Cercopithecus diana*, *Colobus polykomos*, *C. badius*, *C. verus*) during travel compared to foraging (Table 1). Only the terrestrial mangabey leaped more during foraging due to the fact that travel is an overwhelmingly quadrupedal activity on the ground.

### Body size and forest strata

The amounts of locomotor time (1) overall, (2) during travel, and (3) during foraging each species spent in each forest layer are listed in Table 2. Five monkeys in this study are predominately arboreal. The sixth, the sooty mangabey, spends the majority of its time traveling and foraging (as well as engaging in postural activities) on the ground or in the shrub layer. Nevertheless, all of the Tai monkeys were observed, to varying extents, on the ground. Table 2 reveals that there is an overall vertical hierarchy in the forest. *Colobus badius* and *C. polykomos* are main canopy monkeys, whereas *C. verus* and *Cercopithecus campbelli* tend to confine their locomotion to the understory and/or below. *Cercopithecus diana* spends approximately equal time in the main canopy and the understory. *Cercopithecus diana* was the only species that used the layers of the forest in similar proportions during travel and foraging.

How does strata use during locomotion relate to the relative number of different-sized substrates at different forest levels? Table 3 summarizes the relative proportions of substrate types (e.g., boughs, branches, and twigs) at each 10-m interval. The greatest density of boughs is found between 21 and 30 m (10.1% of supports were boughs) and between 31 and 40 m (6.1% of all supports were boughs). These height intervals, which correspond to the main canopy (3+ and 3-) were clearly the strata used

TABLE 2. Strata use during overall locomotion, travel and foraging<sup>1</sup>

Strata	4	3+	3-	2	1	Ground	N
<i>Colobus badius</i>							
Overall	2.4	32.9	41.5	22.8	.3	.1	1,466
Travel	2	36.6	44.3	16.9	.1	—	797
Forage	2.8	28.1	37.8	30.5	.6	.2	669
<i>Colobus polykomos</i>							
Overall	2.5	32.4	36	27.8	.9	.4	918
Travel	.7	32.3	43.5	23.2	—	.2	538
Forage	4.7	32.6	26.8	33.4	1.8	.5	380
<i>Colobus verus</i>							
Overall	.2	3.3	19.4	63.9	7.5	5.7	508
Travel	—	4.3	23.9	61.4	4.9	5.6	306
Forage	.5	1.9	12.9	67.3	11.9	5.5	202
<i>Cercopithecus diana</i>							
Overall	1.3	18.4	31.3	43.6	3.2	2.2	1,553
Travel	1.2	13.6	38.4	43.4	1.7	1.7	242
Forage	.9	19.2	30.1	44.2	3.3	2.3	1,311
<i>Cercopithecus campbelli</i>							
Overall	—	1.7	5	54.5	18.6	20.2	596
Travel	—	5.2	5.2	48.9	8.3	32.3	96
Forage	—	1	5	55.8	20.4	17.8	500
<i>Cercocebus atys</i>							
Overall	—	.8	2.1	8.2	12.7	76.2	466
Travel	—	1.5	3.6	5.8	2.9	85.5	137
Forage	—	.6	1.5	9.7	16.7	71.4	329

<sup>1</sup> Data under each column are the percentages of locomotor time overall, during travel, and during foraging spent in each stratum. 4, Emergent layer; 3+, upper main canopy; 3-, lower main canopy; 2, understory; 1, shrub layer. All interspecific comparisons of strata use during overall locomotion are significant except *Colobus badius* × *C. polykomos* [G = 9.3]. All interspecific comparisons of locomotion during travel are significant except *C. badius* × *C. polykomos* [G = 11.8]. All interspecific comparisons of locomotion during foraging are significant except *C. badius* × *C. polykomos* [G = 16.7]. All intraspecific comparisons of strata use during travel versus foraging are significant except *Cercopithecus diana* [G = 10.4].

most often by the largest arboreal monkeys (*Colobus polykomos* and *C. badius*). The next largest monkey, *Colobus verus*, concentrated its activity in the understory which is dominated by twigs (69.6%) and, to a lesser extent, branches (25.8%).

*Cercopithecus diana* and *C. campbelli* are similar in body size but differ in their strata

TABLE 3. Distribution of support types at 10-meter intervals<sup>1</sup>

Height (m)	Bough	Branch	Twigs	Total
>40	0	21.3	78.7	169
31-40	6.1	30.4	63.5	1,170
21-30	10.1	30.7	59.1	2,249
11-20	4.6	25.8	69.6	3,093
0-10	1.4	41.7	56.9	2,878
Totals	481	3,082	5,996	9,559

<sup>1</sup> The number expressed is the proportion of each support type at each 10-meter interval (from McGraw 1996).

use. The diana monkey, which is predicted to be less restricted by the availability of boughs than larger monkeys, does appear to use more canopy levels—dividing most of its time relatively evenly between the understory and the main canopy. Campbell's monkey, on the other hand, confines almost 94% of its locomotion to the understory and below. The difference between these two guenons is strong evidence that body size and support availability alone do not necessarily predict strata use and, consequently, specific patterns of locomotion. The forest floor is the most frequently used substrate of *Cercocebus atys*. That this species did not seek out those forest levels with larger supports to move in (i.e., main canopy) demonstrates that the tendency to remain at low levels in the forest is more important than the need to travel in those layers with more boughs. Therefore, while some species do show a tendency to be limited by substrate size (e.g., *Colobus badius* and *C. polykomos*) others do not (*Cercopithecus diana*).

#### Locomotion and forest strata

**Climbing.** The amount of time each species spent climbing in each forest stratum during both travel and foraging is presented in Table 4. With one exception (*Colobus badius*), the greatest frequencies of climbing during travel occurred in the understory. Little, if any climbing was observed in the emergent level in any species. During foraging, all species except *Cercocebus atys* climbed most often in the understory. All species except *Cercopithecus diana* climbed in the shrub layer more during foraging than during travel, but there was little consistency in the manner that species climbed more or less in the main canopy layers during travel and foraging.

**Leaping.** The amount of time each species spent leaping in each forest stratum during both travel and foraging is presented in Table 5. The data show that the spatial arrangement of supports alone does not predict where the six monkeys will leap most often. During travel, the three smallest species (*Cercopithecus campbelli*, *C. diana*, and *Colobus verus*) leaped most often in the understory. In contrast, the two larger arbo-



TABLE 4. Climbing and strata use during travel and foraging<sup>1</sup>

Strata	4	3+	3-	2	1	Ground	N
<i>Colobus badius</i>							
Travel	1	28	44	27	—	—	96
Forage	1	18	37	42	2	—	143
<i>Colobus polykomos</i>							
Travel	—	13	41	46	—	—	37
Forage	—	16	20	62	2	—	89
<i>Colobus verus</i>							
Travel	—	—	5	84	11	—	19
Forage	—	—	12	71	17	—	42
<i>Cercopithecus diana</i>							
Travel	—	7	13	67	13	—	15
Forage	—	15	28	50	7	—	272
<i>Cercopithecus campbelli</i>							
Travel	—	—	—	100	—	—	3
Forage	—	1	4	61	34	—	82
<i>Cercocebus atys</i>							
Travel	—	—	—	100	—	—	4
Forage	—	—	—	19	76	5	54

<sup>1</sup> Data in each column are the percentage of climbing during either travel or foraging observed in each stratum. 4, Emergent layer; 3+, upper main canopy; 3-, lower main canopy; 2, understory; 1, shrub layer. Significant interspecific comparisons of strata used during travel: *Colobus badius* × *Cercopithecus diana* [G = 16.3], and *Colobus badius* × *C. verus* [G = 31.2]. All interspecific comparisons of strata used during foraging are significant except *Cercopithecus diana* × *Colobus polykomos* [G = 7.1], *Colobus badius* × *Cercopithecus diana* [G = 9.1], *Colobus badius* × *C. polykomos* [G = 9.4], and *C. verus* × *Cercopithecus campbelli* [G = 6.1]. All intraspecific comparisons of strata used for climbing during travel versus foraging yielded nonsignificant results. Significance tests were not performed for those cases involving N < 10.

TABLE 5. Leaping and strata use during travel and foraging<sup>1</sup>

Strata	4	3+	3-	2	1	Ground	N
<i>Colobus badius</i>							
Travel	3	35	44	18	—	—	163
Forage	3	33	33	29	1	—	99
<i>Colobus polykomos</i>							
Travel	—	30	35	35	—	—	82
Forage	4.5	20	24	47	4.5	—	49
<i>Colobus verus</i>							
Travel	—	4	17	71	8	—	76
Forage	—	—	11	79	11	—	28
<i>Cercopithecus diana</i>							
Travel	2	10	20	68	—	—	40
Forage	1	11	30	51	7	—	121
<i>Cercopithecus campbelli</i>							
Travel	—	—	—	80	20	—	5
Forage	—	—	—	65	35	—	26
<i>Cercocebus atys</i>							
Travel	—	—	—	—	100	—	1
Forage	—	—	—	50	—	50	4

<sup>1</sup> Data under each column are the percentage of leaping during travel or foraging observed in each stratum. 4, Emergent layer; 3+, upper main canopy; 3-, lower main canopy; 2, understory; 1, shrub layer. All interspecific comparisons of strata used during travel are significant except *Cercopithecus diana* × *Colobus verus* [G = 6.3], *C. badius* × *C. polykomos* [G = 10.4], and *C. polykomos* × *Cercopithecus diana* [G = 12.7]. All interspecific comparisons of strata used during foraging are significant except *Cercopithecus diana* × *Colobus polykomos* [G = 2.9], *Colobus badius* × *C. polykomos* [G = 6.5], *C. verus* × *Cercopithecus campbelli* [G = 7.1], and *C. diana* × *Colobus verus* [G = 11.8]. All intraspecific comparisons of strata used for leaping during travel compared to foraging are not significant. Significance tests were not performed in those cases involving N < 10.

real monkeys leaped equal (*Colobus polykomos*) or significantly greater (*C. badius*) amounts in the lower main canopy as they did in the understory. Leaping during travel by any species was rarely observed in the emergent level. During foraging, four of the five arboreal monkeys leaped most often in the understory.

**Quadrupedal running.** The amount of time each species spent running in each forest stratum during both travel and foraging is presented in Table 6. During both maintenance activities, most running in the large arboreal monkeys was confined to the main canopy layers. The olive colobus generally avoided running in the shrub layer and upper reaches of the forest, preferring the understory and low main canopy instead. During travel and foraging, *Cercopithecus diana* used the middle forest layers most evenly. *Cercopithecus campbelli* ran most frequently on the ground and understory

(travel) or the ground and the shrub layer (foraging). During travel, running in the emergent and shrub layers was rarely observed in any species.

**Quadrupedal walking.** The amount of time each species spent walking in each forest stratum during travel and foraging is presented in Table 7. During foraging, four of the species demonstrated patterns similar to those observed during travel: *Cercocebus atys* walked largely on the ground, *Colobus verus* and *Cercopithecus campbelli* preferred the understory, and *Colobus badius* preferred the low main canopy. *C. polykomos* walked the same amount in the understory during foraging and travel, but walked more often at the top of the main canopy during foraging than during travel. Most walking in *Colobus verus* was observed in the understory during both maintenance activities. *Cercopithecus diana* walked more in the low main canopy during travel, but generally

TABLE 6. Quadrupedal running and strata use during travel and foraging<sup>1</sup>

Strata	4	3+	3-	2	1	Ground	N
<i>Colobus badius</i>							
Travel	4	38	47	11	—	—	73
Forage	13	47	34	4	—	2	32
<i>Colobus polykomos</i>							
Travel	1	38	43	17	—	1	213
Forage	2	40	40	15	—	3	55
<i>Colobus verus</i>							
Travel	—	3	28	51	—	18	90
Forage	1	—	19	43	8	29	21
<i>Cercopithecus diana</i>							
Travel	—	19	46	30	—	5	57
Forage	5	23	27	33	1	11	102
<i>Cercopithecus campbelli</i>							
Travel	—	—	9	23	4	64	22
Forage	—	—	—	1	49	50	24
<i>Cercocebus atys</i>							
Travel	—	—	14.5	14.5	—	71	7
Forage	—	—	—	—	50	50	2

<sup>1</sup> Data under each column are the percentage of quadrupedal running during travel or foraging observed in each stratum. 4, Emergent layer; 3+, upper main canopy; 3-, lower main canopy; 2, understory; 1, shrub layer. All interspecific comparisons of strata used during travel are significant except *Colobus badius* × *C. polykomos* [G = 1.5] and *C. badius* × *Cercopithecus diana* [G = 9.8]. All interspecific comparisons of strata used during foraging are significant except *Colobus badius* × *C. polykomos* [G = 5.3], *Cercopithecus campbelli* × *C. diana* [G = 3.3], *Cercopithecus campbelli* × *Colobus verus* [G = 3.3], and *Cercopithecus diana* × *Colobus verus* [G = 11.8]. All intraspecific comparisons of strata used for quadrupedal running during travel versus foraging are not significant. Significance tests were not performed in those cases involving N < 10.

distributed this locomotor mode fairly evenly throughout strata 2 and 3. Most walking in *C. campbelli* was observed in the understory or below. Campbell's monkey walked more in the shrub layer while foraging. The terrestrial sooty mangabey used the ground most often.

**Body size and support use.** The supports used by each species during overall locomotion, during travel, and during foraging are summarized in Table 8. During both travel and foraging, the largest supports (boughs) were used most by the largest arboreal monkeys and least often by the smallest (*Cercopithecus campbelli*). *Colobus verus* used fewer boughs and more branches than its larger congeners. *Cercopithecus diana* and *C. campbelli* showed markedly different patterns of support use, a phenomenon most likely related to species-specific foraging strategies. The diana monkey was the most frequent user of twigs, while Campbell's

TABLE 7. Quadrupedal walking and strata use during travel and foraging<sup>1</sup>

Strata	4	3+	3-	2	1	Ground	N
<i>Colobus badius</i>							
Travel	1	41	43	15	—	—	430
Forage	3	29	39	29	—	—	353
<i>Colobus polykomos</i>							
Travel	1	30	49	20	—	—	198
Forage	8	42	27	22	1	—	186
<i>Colobus verus</i>							
Travel	—	6	28	61	4	1	119
Forage	—	4	13	68	11	4	110
<i>Cercopithecus diana</i>							
Travel	1.5	13	45	39	1.5	—	128
Forage	1	21	31	43	2	2	797
<i>Cercopithecus campbelli</i>							
Travel	—	8	4	53	9	26	66
Forage	—	6	5	52	17	20	388
<i>Cercocebus atys</i>							
Travel	—	2	4	2	2	90	125
Forage	—	1	2	7	5	85	267

<sup>1</sup> Data under each column are the percentage of quadrupedal walking during travel or foraging observed in each stratum. 4, Emergent layer; 3+, upper main canopy; 3-, lower main canopy; 2, understory; 1, shrub layer. All interspecific comparisons of strata used during travel are significant except *Colobus badius* × *C. polykomos* [G = 8.3]. All interspecific comparisons of strata used during foraging are significant. All intraspecific comparisons of strata used for quadrupedal walking during travel versus foraging are significant except *Colobus verus* [G = 12.8], *Cercopithecus campbelli* [G = 10.9], and *Cercocebus atys* [G = 6.4].

monkey was the most frequent user of branches. In addition, diana monkeys used boughs nearly twice as often as Campbell's monkey. *Cercocebus atys* is clearly the outlier, spending over 65% of its foraging time and over 80% of its traveling time on the ground. Thus, while the large arboreal monkeys were the most frequent users of large supports, smaller monkeys demonstrated more varied use of different-sized supports; e.g., small monkeys of similar size did not use all support types in similar proportions.

#### Support size and maintenance activities

Intraspecific comparisons of supports used during foraging versus traveling provide strong evidence that larger supports are used more during travel while smaller supports are used more during foraging (Table 8). Pairwise comparisons revealed significant differences in every case, and a clear trend is evident among all species. *Colobus polykomos* used boughs nearly twice as much during travel than during foraging. Branches and twigs were used less frequently during

TABLE 8. Support use during overall locomotion, travel and foraging<sup>1</sup>

Species	0	1	2	3	4	5	N
<i>Colobus badius</i>							
Overall	.14	1.3	38.6	28.6	31.4	—	1,466
Travel	—	1.1	48.9	24.1	25.8	—	797
Forage	.3	1.3	26.3	33.6	38.4	—	669
<i>Colobus polykomos</i>							
Overall	.4	.6	48.3	25.7	25	—	918
Travel	.2	.4	52.6	23.6	23.2	—	538
Forage	.5	1.3	27.4	36.6	34.2	—	380
<i>Colobus verus</i>							
Overall	5.5	1.7	24.2	38.1	30.3	.2	508
Travel	5.8	2.2	31.9	39.3	20.4	.3	306
Forage	5	.9	11.4	38.1	44.1	.5	202
<i>Cercopithecus diana</i>							
Overall	2.1	1.3	21.7	34.2	40.6	.1	1,553
Travel	1.7	.4	43.8	24.8	29.3	—	242
Forage	2.1	1.3	17.3	36.8	42.3	.15	1,311
<i>Cercopithecus campbelli</i>							
Overall	15.6	.2	12.7	38.7	28.3	4.4	596
Travel	28.1	1	23.9	36.5	6.3	4.2	96
Forage	13.2	.4	10.6	38.6	32.8	4.4	500
<i>Cercocebus atys</i>							
Overall	70.6	2.3	7.6	12.7	2.3	4.5	466
Travel	80.4	1.4	5.8	3.6	2.9	5.8	137
Forage	65.7	2.4	8.5	17	2.12	4.3	329

<sup>1</sup> Data under each column are the percentage that each support type was used during overall locomotion, travel, and foraging. 0, Ground; 1, vertical trunk; 2, bough; 3, branch; 4, twig; 5, other. All interspecific comparisons of overall support use are significant except *Colobus badius* × *C. polykomos* [G = 6.5]. All interspecific comparisons of support use during travel are significant except *Colobus badius* × *C. polykomos* [G = 4.2], *C. badius* × *Cercopithecus diana* [G = 13.8], and *C. polykomos* × *Cercopithecus diana* [G = 9.5]. All interspecific comparisons of support use during foraging are significant except *Colobus badius* × *C. polykomos* [G = 2.1] and *Colobus verus* × *Cercopithecus diana* [G = 8.8]. All intraspecific comparisons of support use during travel versus foraging are significant.

travel. Although not statistically significant, *Colobus badius* showed the same trend, using boughs (48.9%) more during travel than during foraging (26.3%). *Colobus verus* used boughs nearly three times as often during travel while twigs were used roughly twice as frequently during foraging. *Cercopithecus campbelli* used the largest possible support (the ground) almost twice as frequently during travel, while twigs were used nearly five times as often during foraging. *Cercopithecus diana* also used boughs much more frequently during travel (43.8%) than during foraging (17.3%). Although a large percentage of foraging in the sooty mangabey occurred on the ground (65.7%), an even larger (80.4%) percentage of traveling took place on this substrate. This variation leads one to suspect that interspecific differ-

ences in support use may become amplified during travel.

## DISCUSSION

This section reviews the main points of the study and places them within the context of comparative data. The purpose is to determine the extent that these results agree with those of Fleagle and Mittermeier (1980) and Gebo and Chapman (1995), as well as to explore general reasons why some cercopithecoid behaviors and relationships differs from those operating in other primate groups. The most significant exception concerns the issue of leaping, and special emphasis is given to how this locomotor mode is related to body size and life in the canopy of Old World forests.

### Comparison with previous studies

In a number of ways, these data support the findings of Fleagle and Mittermeier (1980) and Gebo and Chapman (1995). First, the relationship between locomotion and maintenance activities appears to be quite strong. In the Surinam, Kibale, and Tai monkey groups, climbing is more common during foraging, and (with one exception) leaping is more common during travel. Second, all monkeys generally tend to use larger supports more during travel than during foraging, as predicted. This is most likely due to the (1) location of preferred food items and (2) the avenues chosen for travel. If the majority of food is located in the outer reaches of a tree's crown, then accessing fruit, leaves or insects requires negotiation of smaller, less stable supports (reflected not only in support use during foraging, but also in the locomotor behaviors used on these support types). Even the sooty mangabey, which spends the majority of its locomotor time on the ground, uses smaller supports during feeding because it frequently climbs understory saplings to search for food. During travel, monkeys are able to choose larger, more stable supports which tend to be found toward the center of a tree or on the forest floor. Campbell's monkey, which spends a high percentage of its foraging time in the discontinuous understory, frequently drops to the ground for long distance travel. These data suggest, therefore, that while sympat-

ric species may eventually feed on different support types, the supports used to get to feeding localities are more similar.

Third, as predicted, the largest arboreal monkeys use the largest support (boughs) more often than do the smaller monkeys during both travel and foraging. Support use among the smaller monkeys is more complex. For example, despite weighing less, *Cercopithecus diana* used boughs more often than did *Colobus verus* during both travel and foraging. It is possible that elevated use of branches and twigs by the olive colobus is due to this species' tendency to move among supports that afford the most cover (Oates and Whitesides, 1990). This could explain its aversion to boughs which tend to be found in the open. The smallest monkey (*Cercopithecus campbelli*) used boughs the least of any species, but also used the smallest support (twigs) the least amount as well. This is most likely due to Campbell's monkey penchant for foraging at forest levels below 10 m, where branches are most abundant. Thus, while it is true that large monkeys use the largest supports more than small monkeys, the use of medium and small supports by smaller-bodied monkeys is influenced greatly by species-specific foraging and travel strategies. Similar patterns were observed among the cercopithecids at Kibale: Although the largest support was used most often by the largest monkey, there was a weaker correlation between body size and medium-to-small supports (Gebo and Chapman, 1995). Among quadrupedal platyrrhines (Fleagle and Mittermeier, 1980), support size does increase with body size.

In general, large arboreal monkeys appear more limited to those forest layers with large substrates while smaller monkeys are not. This point is supported by the fact that the three smallest monkeys, not as limited by the abundance of preferred substrates and, therefore, able to choose from more strategies, have each adopted quite distinct patterns of strata use, support use, and consequently, locomotion. *Cercopithecus diana* spends the majority of its time in the middle forest layers, *Colobus verus* is an understory specialist, while *Cercopithecus campbelli* makes its living in the understory, the shrub layer, and on the ground. The two

large *Colobus* monkeys (*Colobus polykomos* and *C. badius*), as predicted, spend the majority of their locomotor time being quadrupedal in the main canopy where bough density is greatest.

Among the larger arboreal species, high climbing frequencies generally appear to be associated with the understory. This is due to the abundance of more vertically oriented supports which limit the ability of large monkeys to be quadrupedal. Elevated frequencies of climbing in the large colobines were also observed in the main canopy layers; climbing is frequently observed in the terminal branches of tree crowns where supports are too thin and flexible to allow for quadrupedal movement. A similar argument may account for the increased levels of climbing seen in the shrub layer during foraging in all but one species. There, as monkeys move from main canopy layers to the ground (and vice versa), climbing is frequently the only locomotor alternative (with the possible exception of vertical drops or leaps). In the smaller arboreal forms and in the terrestrial mangabey, the majority of climbing took place in the understory and shrub layers. Thus, climbing is generally associated with the understory for all species.

At Kibale, Gebo and Chapman (1995) found that as among the Surinam platyrrhines (Fleagle and Mittermeier, 1980), most quadrupedalism took place in the mid- and upper canopy levels. The relationship between quadrupedalism and different forest strata in the Tai cercopithecids appears more complex. Although the highest frequencies of quadrupedal walking and running in the two large arboreal monkeys generally occurred in the lower main canopy (where bough density is greatest), the smaller arboreal monkeys were much more diverse in their quadrupedalism. That high frequencies of quadrupedalism were employed in the understory (*Colobus verus*), in the shrub layer (*Cercopithecus campbelli*), and in the main canopy (*Cercopithecus diana*) by three small, but similarly sized monkeys suggests that small body size does not necessarily limit a monkey to a particular strategy. For example, preliminary data (Adachi, personal communication) reveal that *C. campbelli*'s diet consists largely of insects which it seeks at levels



below the main canopy. Campbell's monkey does leap at levels below the main canopy but, more often than not, forages using slow quadrupedalism as it carefully scans the dimly lit understory for fruit and insects. This method of insect foraging would seem to favor cautious, slow progression. That this monkey spends the majority of its time in the understory, yet does not engage in high frequencies of leaping or climbing further attests to its preference for quadrupedalism and implies careful, deliberate support choice.

The relationship between body size and climbing (1) during travel and (2) among colobines fits the pattern seen in other primate groups: Larger monkeys climb more than smaller monkeys. However, when overall locomotion is considered, the smaller guenons climbed more than the larger colobines. In the case of *Cercopithecus diana*, this is most likely due to the high frequencies that the diana monkey climbs while foraging (compared to the frequency it climbs during travel). More than any other species, the diana monkey does not restrict its activity to a particular forest level, but rather continually moves between the main forest strata. A highly active primate, the diana monkey spends the least time resting and the second greatest amount of time feeding and foraging (Table 9). Driven by the requirements of a diet consisting of large amounts of ripe fruit and insects (Wachter et al., 1997), the diana monkey is required to engage in considerable vertical as well as horizontal movement through all canopy layers. Struhsaker (1980) observed similar behavior in the small-bodied red-tailed guenon (*Cercopithecus ascanius*) at Kibale. In comparing its movement to that of the larger red colobus monkey, Struhsaker noted that, "the greater proportion of time spent by red tails in climbing is related to differences in the density and distribution patterns of their food as compared with that of the red colobus. Arthropods and fruit of optimal ripeness occur in lower densities and have a more scattered distribution than do most of the red colobus foods. The redtails, therefore, spend more time climbing in search for their food than do the red colobus" (1980:43). The same is most likely true for *Cercopithe-*

TABLE 9. Overall activity budgets<sup>1</sup>

Species	Feed	Rest	Social	Travel	Forage	N
<i>Colobus badius</i>	29.1	29.9	6.3	18.9	15.8	4,196
<i>Colobus polykomos</i>	34.9	33.9	5.3	15.1	10.8	3,538
<i>Colobus verus</i>	26.5	35	6.7	19.1	12.7	1,595
<i>Cercopithecus diana</i>	33.2	8.8	1.2	28.5	28.3	3,539
<i>Cercopithecus campbelli</i>	35.5	20.2	2.8	6.7	34.8	1,437
<i>Cercocebus atys</i>	38.8	18.5	7.9	10.3	24.5	1,343

<sup>1</sup> Data under each column are the percentages of 3-minute time points that each species engaged in each maintenance activity. All interspecific comparisons of overall activity budgets are significant.

*cus diana* at Tai. That the diana monkey must climb across a wide array of supports in search of patchily distributed food is supported by Pope and Strasser (1995:174) who note, "the diana guenon moves on a very complex network of substrates and consequently shows great versatility in its use of types of symmetrical gaits."

The most striking exception to the patterns demonstrated by Fleagle and Mittermeier (1980) concerns leaping. During both travel and foraging, the species that leaped most were the largest arboreal monkeys (*Colobus* spp.). Even among the smaller cercopithecines, the larger *Cercopithecus diana* leaped significantly more during travel and foraging than did the smaller *Cercopithecus campbelli*.<sup>2</sup> Furthermore, although the majority of leaping in the smaller monkeys occurred in the understory, the two largest leapers did not leap most frequently in the understory (as predicted by Fleagle and Mittermeier, 1980) or in the emergent level (as predicted by Napier, 1967), but rather in the continuous main canopy. Gebo and Chapman (1995) found the same relationship

<sup>2</sup>The Tai Forest contains primates that were not included in this study. Doran (1993) has studied the locomotion of Tai chimpanzees (*Pan troglodytes*). In addition, the greater (*Cercopithecus nictitans*) and lesser spot-nosed guenons (*Cercopithecus petaurista*) as well as Bosman's potto (*Perodicticus potto*) and the dwarf galago (*Galagoides demidovii*) range throughout the Tai Forest, although quantitative data on these species at Tai are not yet available. Reports from the literature indicate that the potto (1.15 kg) is a slow climber (Charles-Dominique 1977; Fleagle 1988), while the dwarf galago (.7 kg) is said to be the most quadrupedal of galagos, occasionally effecting short leaps between nearby branches (Charles-Dominique 1977; Fleagle 1988). When data on chimpanzee locomotion are considered (see Doran, 1993), Fleagle and Mittermeier's (1980) prediction is supported: The largest primate (chimpanzee) leaps least and climbs the most. Without locomotor data on the potto and galago, it is not possible to deduce the pattern at the opposite end of the body size spectrum.

between body size and leaping in the Kibale cercopithecids.

### Leaping in cercopithecids

Because there is considerable variation in body size even among the three *Colobus* species, it is unlikely that the tendency to leap is related to their size, but rather to something else inherent in "being a *Colobus* monkey." Colobines, by definition (but not always in practice), are leaf eaters and all are adept leapers (Napier and Napier, 1985; Fleagle, 1988). Recent surveys have found a strong association between leaping and leaf eating among primates in general (Fleagle and Reed, 1996). Although Tai colobines leap more during travel than foraging, with the exception of *Colobus verus*, they do not do so by much. That is, frequencies of leaping are high during both travel and foraging, and significantly greater than among cercopithecines. This implies that, at least among the two large colobines, leaping may play a comparable role during both activities. If so, then one challenge is to determine what the relationship is between being a leaper and being folivorous.

Is leaping related to the cost of gathering or the method of obtaining leaves? Unlike species who rely on adaptations such as prehensile tails, forelimb suspension, or claws for clinging, it is not clear how this locomotor adaptation might provide a larger feeding sphere (Grand, 1972) than that of an animal with more equal limbs. It is possible that those monkeys who do not spend large amounts of time foraging, maximize their foraging efficiency by minimizing energy expenditure during feeding by leaping. However, whether it is more efficient to be relatively inactive and leap (e.g., *Colobus badius*, *C. polykomos*, and *C. verus*) (Table 9) as compared to being highly active and more of a quadrupedal walker or climber (*Cercopithecus diana*, *C. campbelli*, and *Cercocebus atys*) remains to be demonstrated.

Are elevated leaping frequencies necessarily adaptations to understory living? While it is true that (1) the most frequent leaper (*Colobus verus*) did spend the most time in the understory and (2) frequencies of leaping for all species were higher in the understory, the fact that other species that spent

large portions of time in the understory *did not* leap frequently (e.g., *Cercopithecus campbelli*) and, more importantly, that most leaping among the larger colobines took place in the main canopy and above, is evidence that among these species there is little association between diet, leaping, and understory living. Olive colobus monkeys most likely have greater access to their preferred foods because of their ability to leap within the understory; however, this should be true for any primate that made its living there. While it has been shown that many understory species are frequent leapers, at Tai, some are not. Furthermore, leaves are readily accessible in the main canopy without needing to leap. If this were not the case, we might expect South American howler monkeys to be adept leapers which they are not (Schon Ybarra, 1984; Gebo, 1992). Leaping is, therefore, clearly not related functionally to where leaves are most often found nor is it a prerequisite for understory living.

An alternative way of looking at the question is to ask, If leaping provides such a useful option for moving through the canopy, why don't *Cercopithecus* monkeys do so more often? To be sure, guenons are quite capable of crossing between discontinuous supports or across gaps. Napier (1976:9), however, distinguished the manner that guenons and colobines propel themselves through the air noting that, "In other quadrupedal species, like the guenons (*Cercopithecus*), the differentiation of function between fore and hindlimbs is less pronounced; these monkeys jump rather than leap so that in both take-off and touch down the two sets of limbs play nearly similar roles." The fact that guenons "jump" rather than "leap," as a result of more equal limb lengths, may reflect the premium put on highly adept quadrupedalism. If a monkey obtains the majority of its food by actively foraging across the widest array of possible supports, and if this animal does not possess any other specialized positional adaptations, then it had better be the best arboreal quadruped possible. Relatively short limbs of equal length may enable more adept quadrupedal behavior (Schmitt, 1995); otherwise more arboreal cercopithecines would have developed elongated hindlimbs. Enhanced leaping capabilities are therefore

sacrificed for highly efficient quadrupedalism. Conversely, colobus monkeys who do not need to negotiate as wide array of supports as frequently as guenons can develop leaping abilities without as great a trade-off.

Can differences in body size account for leaping in colobines? Fleagle (1985) argued that small-bodied primates will encounter more forest gaps (which can only be crossed by leaping) than a larger-bodied monkey and that, "larger animals will more frequently encounter supports too narrow and too weak to support their larger bodies and would more readily need to suspend themselves below multiple branches both for support and balance (1985:13)." Smaller-bodied primates (who are more adept quadrupeds) may encounter more gaps, but they also may be better able to negotiate further out on and across the terminal branches of adjacent trees, thereby decreasing the size of potential gaps and minimizing travel distance without having to leap as often. Moreover, because colobines have not evolved any adaptations for habitually suspending themselves below branches (as have large-bodied platyrrhines such as the atelines), these large monkeys will encounter many occasions in which leaping provides the best way to negotiate the various forest strata. Ripley (1967), for example, argued that leaping allowed Asian leaf monkeys to *most* efficiently move through the main canopy. Indeed, the ability to leap should be advantageous for *any* large monkey that spends significant time in the main canopy and does not possess other more specialized adaptations (e.g., brachiation, prehensile tail).

The main canopy, which may be more "continuous" than the understory, can hardly be considered a network of contiguous, interlocking supports. Like their counterparts in the understory, main-canopy monkeys are frequently faced with gaps of varying sizes throughout all layers of forest (Cannon and Leighton, 1994; Jans et al., 1993). The endpoints of these gaps are often not the large, stable supports (e.g., vertical trunks) that are common in the understory, but rather the thin, flexible twigs found in the terminal reaches of adjacent tree crowns. Even when two adjacent trees appear to be continuous (i.e., there is no gap between them), a large

monkey moving through them may judge adjacent supports too narrow and weak to withstand quadrupedal or climbing locomotion and may, therefore, leap farther toward the center of a tree crown where supports tend to be larger and more stable. This may also be reflected in the different manners that colobines and cercopithecines leap and jump, respectively: Most often, colobus monkeys aim for general areas, and their landings are frequently characterized by a monkey crashing into a number of supports and grabbing with all four limbs. Guenons appear much more precise in their landing patterns (Struhsaker, 1975).

In the Old World forest, the largest monkeys tend to be main-canopy leaf eaters. Large primates lacking enhanced brachiating skills or prehensile tails, who are also less able and (because of their diet) not as often required to negotiate small supports as lighter monkeys, should benefit greatly if they can move through the canopy by crossing above or between supports considered too small. Leaping, which provides this means of transport, should be particularly adaptive if these monkeys make their living primarily in the main canopy.

In surveying the locomotion and habitat use of African monkeys, Napier (1962) suggested that leaping evolved as an adaptation to movement in the main canopy. For cercopithecoid monkeys, it appears he was correct. While selection would certainly favor primates that could leap amid the vertically oriented supports in the understory, it is equally plausible that the evolution of leaping capabilities arose in the main canopy which, although it is more horizontally continuous, still contains many gaps and poses a number of problems for large animals that cannot brachiate, are not prehensile, and are less able to walk out on interlocking, but small terminal branches than are smaller monkeys.

As more field data become available, it is increasingly clear that the relationship among body size, positional behavior, and habitat use is very complex. Considering the adaptive diversity of primates, this should not be surprising. The most interesting challenge will be explaining this complexity. Are differences in forest structure between the

Neo- and Paleo-tropics responsible for the manner that platyrrhine and catarrhine monkeys have responded morphologically to their arboreal environments (e.g., Emmons and Gentry, 1983)? Can other selection pressures (e.g., predation pressure) explain why large-bodied cercopithecids leap so much in the main canopy (Gebo and Chapman, 1995)? Hopefully, additional quantitative field data on free-ranging primates will provide the answers to these and related questions.

### SUMMARY

1. Data are reported on the relationship among locomotor behavior, body size, and habitat use of six cercopithecoid monkeys in the Tai Forest, Ivory Coast.
2. Body size does not consistently predict leaping frequencies. During both travel and foraging, the species that leaped most (colobines) were the largest arboreal monkeys. Among colobines, the smallest leaped the most. Among cercopithecines, the larger *Cercopithecus diana* leaped less than the smaller *C. campbelli*.
3. During both travel and foraging, colobines generally climbed more than cercopithecines. Larger colobines climbed more than smaller colobines, but smaller cercopithecines did not climb less than larger cercopithecines.
4. Climbing is more frequent during foraging, and with one exception (*Cercocebus atys*), leaping is more common during travel.
5. In general, large monkeys tend to frequent those forest layers with large substrates, while smaller monkeys, less restricted by substrate abundance, are more diverse in their individual locomotor strategies and canopy use.
6. High frequencies of leaping are not necessarily confined to the understory. Most leaping in the larger colobines took place above the level of the understory. Not all understory specialists are frequent leapers.
7. Larger monkeys do not always use larger supports than do smaller monkeys.
8. Larger supports are generally used during travel, while smaller supports are used during foraging.

9. A general rule about body size, leaping, and canopy use for anthropoid monkeys is not tenable. In the New World, leaping is seen most in small monkeys who frequent the understory while in the Old World, leaping is more common in larger, main-canopy monkeys.

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